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SOUTH AMERICAN *ANOLIS* (SAURIA, IGUANIDAE): TWO NEW SPECIES OF THE *PUNCTATUS* GROUP

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Anolis punctatus Daudin is the earliest discovered, most widely distributed, and morphologically the central member, of a group of forest anoles in South America. The males of *punctatus* (and of its race *boulengeri* O'Shaughnessy) have the rostral swollen, projecting strongly beyond the lower lip. This is the first adumbration of a condition which becomes weirdly emphasized in three species which can be collectively called the proboscis anoles: *A. laevis* Cope, *A. phyllorhinus* Myers and Carvalho, and *A. proboscis* Peters and Orcés. The strange rostral appendages in these three anoles are probably confined to males; at least all known specimens of these species are males.

I here associate with this strange group of anoles, which lengthen the outline of the head by a swelling or soft protuberance, two undescribed species that elongate the bony frame of the snout itself. I associate these two with *punctatus* and its allies because of their general similarity in squamation despite the conspicuous difference in trend. This resemblance may be superficial and convergent, but I find the hypothesis of relationship useful as a provisional organization of the data. It is above all desirable at this moment to arrange and put in order the welter of *Anolis* species — even if somewhat artificially — and this is all the more desirable when still further species must be named.

The two species here described are, for South American species, remarkably distinct. It is usual in South American anoles to be uncertain whether a distinctive population is an unrecognized species or not. No such question exists in these cases. The first species I describe has such strong differences from all described species that I name it:

ANOLIS DISSIMILIS new species

Holotype: CNHM¹ 81369, an adult ♂, Itahuania, upper Rio Madre de Dios, Madre de Dios Province, Peru, Kalinowski coll., 15 October 1954.

Diagnosis: Close to *Anolis proboscis* Peters and Orcés, *A. phyllorhinus* Myers and Carvalho, *A. laevis* (Cope), and *A. punctatus* Daudin. From all of these the new species differs by the absence of any trace of swelling on the snout, by having the ventrals in oblique rather than transverse rows, by its more slender body and longer, narrower head (measured to interparietal scale 1.5 times tibia, ca. $\frac{1}{4}$ snout-vent length).

Description. *Head*: All head scales wrinkled or striate, moderate to large posteriorly, small anteriorly. Seven scales across head

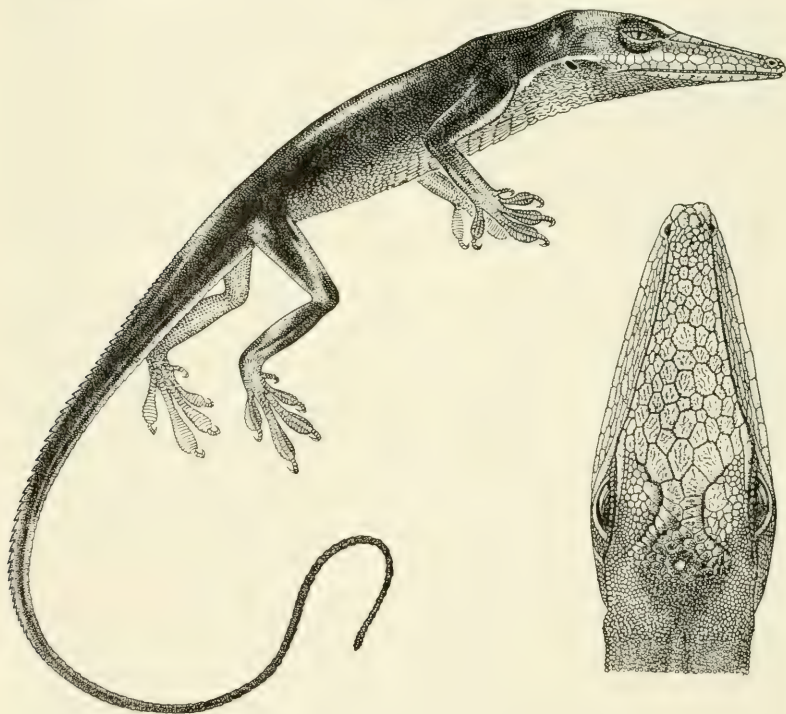


Fig. 1. *Anolis dissimilis* new species. Type, CNHM 81369.

¹For abbreviations see p. 11.

between second canthals. No frontal ridges but a shallow frontal depression. Five scales bordering rostral posteriorly. Rostral partly divided. Nasal scale anterior to canthal ridge, separated from rostral by one scale. Six scales between supranasals.

Supraorbital semicircles broadly in contact, posteriorly partly separated from, anteriorly in contact with the supraocular disks, which consist of approximately nine enlarged scales, the antero-medial one much the largest, the remainder grading posteriorly into granules that become smaller toward the supraciliary margin, anteriorly grading more gradually into the moderately enlarged scales that are in contact with the single supraciliary. The latter short, continued posteriorly by undifferentiated granules, anteriorly fused on both sides with the first canthal. Canthus distinct, canthal scales nine, the second the longest, diminishing gradually forward. Loreal rows five, the lowest row distinctly the largest. Temporal and supratemporal scales subgranular, smooth, grading into the large flat but wrinkled scales that surround the interparietal. Interparietal very much larger than the very small ear, in contact with the supraorbital semicircles.

Suboculars in contact with supralabials, continued behind the eye by granules only, anteriorly in contact with the canthal ridge. Eleven supralabials to the center of the eye.

Mentals distinctly longer than wide, in contact with two elongate throat scales. Sublabials large, wide, four in contact with infralabials on one side, five on the other. Central throat scales elongate, swollen, not keeled.

Trunk: Middorsal scales feebly keeled, distinctly larger than flank granules but grading into them very gradually.

Ventrals larger than dorsals, swollen, smooth, subcycloid, imbricate or subimbricate, arranged in oblique rows.

Gular fan: Fan very large, extending well back on belly, scales narrow, smooth, much longer than ventrals, arranged in close-set lines.

Limbs and digits: Hand and foot scales multicarinate. Largest arm and leg scales unicarinate, smaller than ventrals. About 17 lamellae under phalanges 2 and 3 of fourth toe.

Tail: Tail distinctly compressed, surmounted by a crest of enlarged keeled scales, very uniform in size, that give it a very serrate upper border. Verticils not evident. Lateral caudal scales irregular in size, smaller. Ventral surface of tail covered by two rows of keeled, more elongate scales, smaller than crest scales.

Color: As preserved, essentially uniform dark above, lighter below. No evident pattern.

Size: Snout-vent length 56 mm.

The second species which requires description is most easily recognizable by a very narrow black line extending down the middle of the back. It is therefore described as:

ANOLIS NIGROLINEATUS, new species

Holotype: MCZ 38940, Machala¹, El Oro Province, Ecuador. Luis A. Perez coll.

Paratype: USNM 12280, Guayaquil, Ecuador. No collector listed.

Diagnosis: Similar to *A. punctatus* Daudin but differing in color (lighter and with a black midvertebral line and faint dark markings on flanks and limbs) and in squamation (fewer scales in contact with the rostral, fewer lamellae under fourth toe).

Description. (Paratype differences in parentheses.) *Head:* Head scales moderate, posteriorly smooth, flat, anteriorly weakly keeled; 10 (8) scales across snout between second canthals; frontal depression distinct; 5 (7) scales border rostral posteriorly; anterior nasal scale in contact with rostral; 6 (5) scales between supranasals.

Supraorbital semicircles separated medially by 2 (1) scales from each other on each side and by one row of granules from the well-defined supraocular disk of 10–13 flat scales. One or two elongate supraciliaries bordered medially by polygonal scales and continued posteriorly by granules. Canthus indistinct anteriorly, not forming a single continuous row; 6 loreal rows, subequal.

Temporals and supratemporals both subgranular but the supratemporals longer and grading gradually into the somewhat enlarged scales surrounding the interparietal, which is larger than the ear and separated from the supraorbital semicircles by 3 to 4 scales. Scales posterior to interparietal grading very gradually into nape scales.

Suboculars weakly keeled, in contact with supralabials, anteriorly separated from canthal ridge by 4 (3) scales, posteriorly grading into temporals; 10–11 (8–9) supralabials to center of eye.

Mentals wider than long, deeply indented by first sublabials; 2–3 sublabials in contact with infralabials; 4 gular scales in a

¹The exact locality of collection is in doubt. All specimens in the Perez collection come from El Oro Province and most from the vicinity of Machala but exact data were not kept. It would be preferable to make the USNM specimen the type of this very distinct species except that it is not as well preserved and the locality is not — with any probability — more exact.

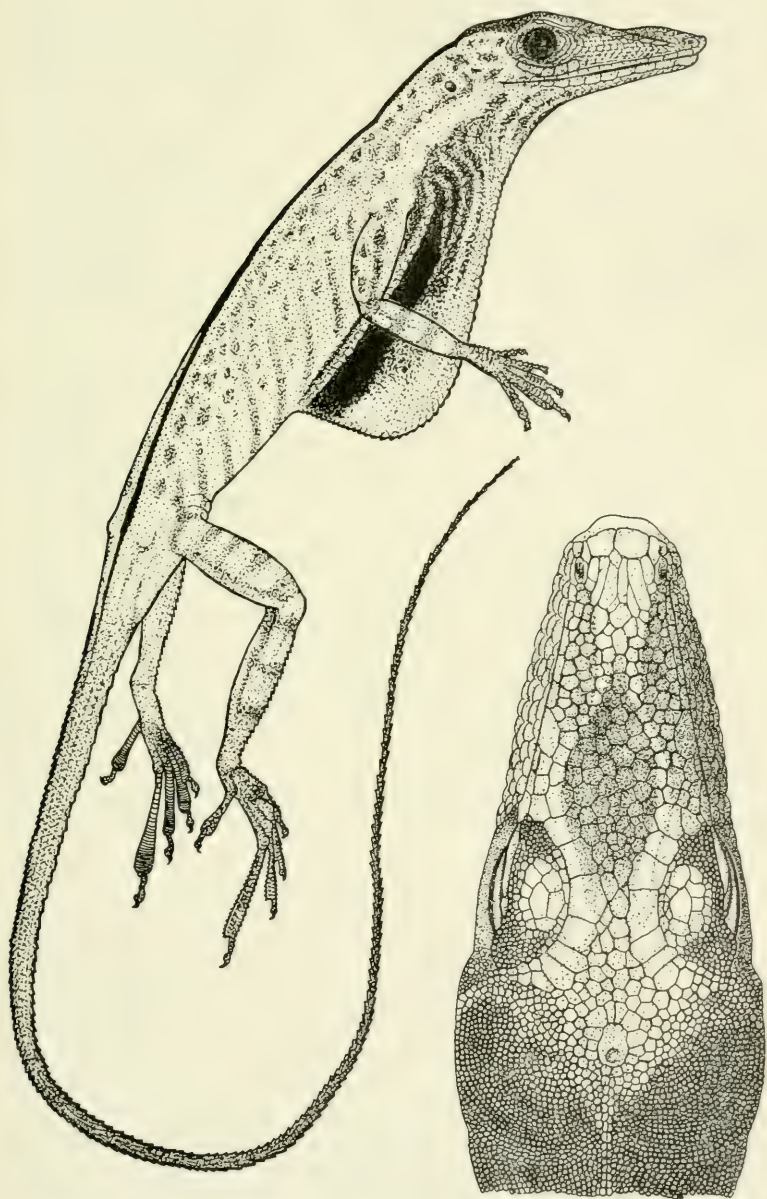


Fig. 2. *Anolis nigrolineatus* new species. Type, MCZ 38940.

gentle forward arc in contact with mentals between sublabials. Gular scales smallest medially grading laterally into sublabials.

Trunk: Two middorsal rows slightly but distinctly enlarged, swollen on nape, grading into flank granules. Ventrals larger, smooth, imbricate.

Gular fan: Very large, extending posteriorly onto more than the first third of the belly, rather densely scaled, the scales at the edge at least the size of the ventrals; smooth, lateral scales smaller.

Limbs: Scales on limbs unicarinate, the largest on hind limb larger than ventrals. Supradigital scales multicarinate. Eighteen lamellae under phalanges ii and iii of fourth toe.

Tail: Compressed, without verticils or dorsal crest. Greatly enlarged postanals present.

Color: As preserved, light brown with faint and broken streaking or reticulation. A black middorsal line two scales wide. Top of head including area around interparietal, but not supratemporals, blackish also. A dark postocular spot. Dewlap light at edge but with a long black spot at base.

Comparative material examined: *A. punctatus* (including the subspecies *boulengeri*): Specimens from many localities in Brasil, Bolivia, Peru, Ecuador and the Guianas.

A. laevis: Type only, ANSP 11368, between Moyabamba and Balsa Puerto on the Rio Huallaga, E. Peru.

A. phyllorhinus: [Type from Borba, lower Rio Madeira, Amazonas, Brasil, not seen], DZ 7118, Rio Tapajoz, Jacareacanga, Pará, Brasil.

A. proboscis: Type only, MCZ 54800, vicinity of Cunuco, N.W. of Mindo, on S. bank of Rio Mindo, Pichincha, Ecuador.

DEFINITION OF THE *Anolis punctatus* SPECIES GROUP

Reference of two new species to a "*punctatus*" group is an obligation to define the group. I attempt this after rather than before describing the new species because of the characteristic difficulties which attend all definitions of species groups within *Anolis* based on externals. This is a genus pervaded with convergence and parallel adaptation to such an extent that only those species series which are also obvious superspecies are clear, discrete units. Just beyond the level of the superspecies it is often not difficult to assemble larger clumps of species that seem evidently related. But here the problem of exclusion rather than inclusion enters. Each added species leads insensibly toward species still more remote from the core species of the putative group.

This situation is well exemplified by the *punctatus* group as here seen. A definition can be proposed but there will be multiple exceptions to certain characters, and certain fringe species which could as well be included or excluded.

A tentative definition (with exceptions) follows: Species of moderate size (but *nigrolineatus* is rather small, and *laevis* relatively large). The snout is produced either by bony structure, swelling, or soft proboscis. The color is probably green in life (usually purples and blues in alcohol), perhaps an exception in *nigrolineatus*. The ear is small and rather ventrally placed (on the level of mouth). The nostril is separated by a single prenasal scale from the rostral. The head scales are flat, pavementose (even in *boulengeri*, which has keeled ventrals and keeling of the dorsal scales). The loreal rows are few (as few as two in *laevis*, as many as seven in *punctatus*). There are no or only a few scales between the supraorbital semicircles (0-2). The interparietal, larger than the ear, is of moderate size (large in *laevis*, *dissimilis* and *proboscis*) and separated from the semicircles by 0 to 4 scales. Suboculars broadly in contact with supralabials. Mental deep, not wide (widest in *nigrolineatus*). Well developed sublabials present. Dewlap large, scales in rows narrowly separated by naked skin (scales *not* in rows in *proboscis*). Middorsals not or not appreciably larger than flank scales (a dorsal crest in *proboscis*). Ventrals smooth (keeled in *boulengeri* which, however, intergrades with smooth-scaled *punctatus*), squarish, transverse. Tail more or less compressed with double row of scales dorsally (a single crest in *dissimilis* and *proboscis*).

This is an extensive list of similarities. However, the differences between species, emphasized above by the exceptions, are as striking as the similarities. They are of many sorts and it is natural to inquire whether the differences are less important than the common characters. It will be useful, therefore, to examine the differences in some detail.

1. *Snout differences.* *A. nigrolineatus* is in this regard not very different from many anoles not closely related to it: the bony structure of the snout itself has been stretched into a tapering, bluntly pointed structure. *A. dissimilis* carries the condition of *nigrolineatus* to an extreme. In contrast, the bony snout of *A. punctatus* is very little modified, but the rostral scale is swollen, protuberant. *A. laevis* has this scale produced into a broad-based flexible appendage. *A. phyllorhinus* has a narrow flexible appendage *above* the triangular rostral scale, this appendage having small granular scales. *A. proboscis* is very similar in the general conformation of the area but the scales on the flexible proboscis are

elongate. The differences here imply, as we have already suggested, that no single linear series can be envisioned; at least two are required. It is, however, possible to suppose that there has been radiation from a central type — perhaps *punctatus*, perhaps an ancestor of *punctatus*.

2. *Interparietal size*. The interparietal is large and in direct contact with the semicircles in so many species of diverse relationships, and the interparietal may so often differ in size and in distance from the semicircles in closely related species that this character is probably of minimal systematic value above the species or superspecies level.

3. *Dewlap squamation*. Again a character subject to much parallel modification and often different within a superspecies. *A. proboscis* is anomalous among the compared species in having a rather uniform squamation of the dewlap rather than scales in distinct, separated rows, but this is probably of no major significance.

4. *Dorsal crest*. *A. proboscis* is again very peculiar in having a dorsal crest of strongly enlarged sub-triangular scales. Such a crest is known in several West Indian so-called giant anoles but is very unusual in mainland species. It does, however, occur in some Guatemalan *A. pentapryon* — whether as an anomaly or a population character is unknown. Special though this feature seems in *A. proboscis*, it is hard to regard this as more significant than the extraordinary proboscis — so like that of *phyllophorus* in which there is no hint of a dorsal crest.

5. *Tail*. The difference between a tail with two rows of scales dorsally and one with a pronounced single crest is a very obvious one. Schmidt (1939), in describing *Anolis barkeri*, and also Myers and Carvalho (1945), in describing *A. phyllophorus*, have made much of the double-rowed condition — a feature which does appear to be unusual in anoles. There is usually in *Anolis* only a single row, whether or not this is produced into a crest. The systematic value of the double row is, however, much diminished by just the case in which Schmidt first used it: *A. barkeri* is a Mexican species which on osteological grounds (Etheridge, 1959) belongs to a very different section of the genus from the South American species in which this peculiarity is otherwise known.

In my judgment these differences, though disturbing at first glance, do not provide serious difficulty for a concept which unites all these species as a unit group. There are strong cross resemblances between species that on other characters would be separated. Thus, *dissimilis* shares with *proboscis* the character,

unusual in South America, of a crested tail, but in the nasal appendage and snout structure *proboscis* resembles *phyllorhinus* and is very different from *dissimilis*.

More awkward for the desiderate goal of taxonomic clarity are the species I have described as "fringe species." These are: *transversalis* (including *buckleyi*); the *solitarius-tigrinus* super-species; *jacare*.

All of these have a double row of scales dorsally on the tail, all have smooth ventrals, few loreal rows, pavementose dorsal head scales, few or no rows between the supraorbital semicircles, suboculars broadly in contact with supralabials, mental deep, not wide, well developed sublabials.

However, the ear is rather large, the color is complex with much cross-barring and spotting. The species of the *solitarius-tigrinus* series are all of small size (40–50 mm snout-vent length), *jacare* and *transversalis* are of moderate size. One peculiar feature which unites this set of species but is untrue or unknown for all those I have referred to the *punctatus* group (untrue for *punctatus*, unknown for the others) is the presence of black pigment in the female dewlap, and its absence in the male structure (which is also somewhat better developed).

To include these species in the *punctatus* group would seem to enlarge it too much; yet a considerable degree of affinity seems probable.

AN EVOLUTIONARY PERSPECTIVE FOR THE *punctatus* GROUP

The first described proboscis anoles — *A. laevis* Cope (Rio Huallaga, Peru) and *A. phyllorhinus* Myers and Carvalho (lower Rio Madeira, Brasil) were Amazonian. This is also true of *A. dissimilis* (on the upper Rio Madre de Dios). But *A. proboscis* Peters is from Pichincha Province in Ecuador, west of the Andean water shed, and *A. nigrolineatus* is from the Pacific lowlands near Guayaquil. *A. punctatus* — the central species of this putative complex — is much more widespread than any of the other species occurring in Amazonia, the Guianas and the forests of eastern Brasil, but neither it nor its western race (with keeled ventrals) — *boulengeri* — ever transgresses into the Trans-Andean Province.

There is, thus, in this species group — if it is a reality — no special geographic pattern except that of being clearly and wholly South American.

That this group is part of a wider autochthonous South American section of *Anolis* has been demonstrated by Richard Etheridge (1959). The species of the *punctatus* group, all examined radio-graphically by him, and a wider circle of forms which include such

species as *boettgeri*, *chloris*, *fasciatus*, *fraseri*, *frenatus*, *insignis*, *jacare*, *latifrons*, *microtus*, *mirus*, *nasofrontalis*, *peraccae*, *pseudotigrinus*, *solitarius*, *squamulatus*, *tigrinus*, *transversalis*, *ventrimaculatus*, are all characterized by possession of posterior caudal vertebrae without transverse processes and without autotomy septa, by the possession of four parasternal chevrons attached to the ribs and by having the lateral arms of the interclavicle divergent from the proximal parts of the clavicles. This is an assemblage of characters that Etheridge has demonstrated to be quite distinctive, and geographically quite coherent, occurring in species of mainland South America (but not those of the West Indies or Malpelo Island) and also in two or three species — *frenatus*, *insignis* and *microtus* — present in extreme southern Central America.

This is a very varied series in everything but these distinctive skeletal characters. These anoles are very different in size (including both dwarfs and giants), and in squamation (Table 2). The series, therefore, has every appearance of being an old assemblage which has had the time to diversify and which has exploited its opportunities.

The autochthonous South American section of *Anolis* shares South America with a group clearly not autochthonous but with its stronghold and center of origin to the north in Central America and Mexico. Though the latter group is clearly an invader from the north, it has reached every part of the total range of *Anolis* in South America. It is amazing that the ranges of these two groups of divergent history should be so closely coterminous in mainland South America.

This invader group is distinguished on Etheridge's osteological characters by having caudal vertebrae *with* caudal autotomy septa, *with* transverse processes which are inclined forward, and *with* an interclavicle the lateral arms of which are in contact with the clavicles. Osteologically, therefore, they are quite distinct from the old South American anoles. In squamation, as Table 2 shows, there is broad overlap. It is, therefore, impossible on external characters to make a separation of the two groups. Indeed, species belonging to the two groups have sometimes been confused with one another, and, in other cases, while the species characters permit ready separation, it will still be impossible *on externals* to allocate the species to group other than randomly.

Yet in bias and trend the two groups do differ. This too is shown in Table 2. In toe lamellae the bias of the alpha group is to higher numbers, that of the beta group to lower numbers. This character

(and probably more obscurely some of the others) is a reflection of an ecological bias in the two groups: the alpha group includes more deep forest, highly arboreal species, the beta group more species of open country — ground, grassland, or bush.

In ecology, as in so much else, there is strong overlap, but the bias or trend is clear. At the extreme of the beta series is an anole that actually lives in or at least takes refuge in holes in the ground (Ruthven, 1922), that in fact has abandoned wholly its arboreal heritage and with it the clinging hairs on the toe lamellae so characteristic of all other anoles. This anole, though only the extreme of its series, is customarily placed in a distinct genus; it is *Tropidodactylus onca*.

At the opposing extreme in the alpha series are probably to be placed the proboscis anoles — which again might be placed in a genus apart did they not seem to achieve their distinctive rostral structure in different ways. Neighbors to these in the extreme wing of the alpha series are *punctatus* and, if I interpret matters rightly, the two new species that are described in this paper.

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Fig. 3. Map of the distribution of *punctatus* group anoles except *A. punctatus* itself. The exact limits of the latter's very wide range are not known.

Table 1
Scale characters of *punctatus* group anoles

	<i>punctatus</i> Daudin 1802	<i>laevis</i> Cope 1875	<i>phyllorhinus</i> Myers & Carvalho 1945	<i>proboscis</i> Peters & Orcès 1956	<i>dissimilis</i> n. sp.	<i>nigrolineatus</i> n. sp.
proboscis	rostral swollen in ♂	soft pro- tuberance covered with small scales (only ♂ known)	leaf-like, laterally compressed with granular scales (only ♂ known)	leaf-like, laterally compressed with elongate scales (only ♂ known)	no modifi- cation of snout (only ♂ known)	no modifi- cation of snout (only ♂ known)
scales between second canthals	11	4 (Cope) ¹	10	9	8	6
scales between semicircles	0-2	0	0	1	0	1-2
scales between interparietal and semicircles	2-4	0	1-2	2	0-1	3
temporals > or < dorsals	<	> (Cope)	=	<	<	=
loreal	4-7	2	4-5	4	4-5	5-7
suboculars in contact with supralabials	+	+	+	+	+	+
labials to center of eye	6-10	?	6-7	9	11	11

¹ Much of the information on *laevis* must come from Cope's original description. Although the type (ANSP 11368) is still in existence, it is in such poor condition that very little can be learned from it. However, the type confirms that there does exist a proboscis anole clearly different from those known by satisfactory material.

Table 1 — Continued
Scale characters of *punctatus* group anoles

	<i>punctatus</i>	<i>laevis</i>	<i>phyllorhynchus</i>	<i>proboscis</i>	<i>dissimilis</i>	<i>nigrolineatus</i>
sublabials in contact with infralabials	2-7	?	5-6	2-3	2-4	2-3
median gular scales in contact with mental	3-4	?	4	2	2	3-4
between sublabials						
mid-dorsal rows	0	0	0	1	gr	(gr)
enlarged				(irregular crest)		
tail crest	double row, no crest	double row, no crest	double row, no crest	+	+	double row, no crest
ventrals ¹	sti	stj	sti	sti	soj	st(i)
lamellae	24-30	?	22-26	19	17	18
4th toe						
toe expansion	wide	narrow	wide	wide	wide	wide

¹ s = smooth; i = imbricate (i) subimbricate; j = juxtaposed; t = transverse; o = oblique; gr = mid-dorsal enlarged, grading into flank scales.

Table 2
Character range in South American anoles

	<i>alpha anoles</i>	<i>beta anoles</i>
number of toe lamellae	14-30 (mode 18-21)	10-27 (mode 14-18)
scales across snout	4-25	7-20
scales between semicircles	0-5 (7 *)	0-4
dorsal scale rows enlarged	0-2	0-12

* Though several alphas range up to five scales between the supraorbital semicircles, the maximum reported here occurs in two exceptional specimens of *A. princeps* Boulenger (= ? *frenatus* Cope).